

Aspects of the Carboniferous Terrestrial Arthropod Community

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ABSTRACT: Although terrestrial arthropods may have formed part of the base of the Carboniferous trophic pyramid, the greatest proportion of primary production in terrestrial ecosystems passes through the decomposer chain. Carboniferous millipedes show a variety of adaptations for inserting themselves into forest litter, except for spined forms which were epigeal; their spines may be broken off or crushed, suggesting encounters with predators. *Arthropleura* may well have been specially adapted to live within the rotting hollow trunks of lycopods, which afforded protection as well as food in the form of the stele. *Arthropleura* may have had a pseudotracheal system. Millipedes and mites played an important role as decomposers, contributing to the soils of the coal forests, and their coprolites are now known from coal balls. The coprolite of *Arthropleura* was probably at least 75 x 40 mm in diameter, but has yet to be found as a fossil. Størmer's view of the eurypterid respiratory structure as a pseudotrachea is accepted, although the structures also show similarities to those of a respiratory plastron. Eurypterids from the Joggins tree stumps are compared with *Dunsophterus*, *Hibbertopterus*, and *Vernonopterus*. It is not clear whether they crawled into the tree stumps, were carried there by predators, or washed in by flooding. Most of the arachnids from overwhelmingly terrestrial faunas like that of Braidwood Mazon Creek are known from only one specimen. This can be interpreted as evidence of high species diversity, possibly coupled with low density, as in modern tropical forests, although statistical analysis is needed. Nine families of arachnids are common to both European and American Westphalian faunas, and this weak evidence supports the better evidence derived from tetrapods for a formerly united Laurasia.

INTRODUCTION

With the exception of the tree-trunk traps of Joggins and elsewhere, knowledge of the Carboniferous terrestrial arthropod community has to be derived from samples of such communities deposited allochthonously by waters of

varying salinity. Such samples may be large, as in the outstanding case of the delta-plain sample of Mazon Creek, with its overwhelmingly terrestrial arthropod invertebrate Braidwood fauna (Richardson and Johnson, 1971). To reassemble the Mazon Creek fauna into its probable community structure would require collaboration among many specialists, and it has not been attempted here. The present account provides notes on the possible biology of the major terrestrial arthropod groups that are present in Carboniferous faunas, with the notable exception of the insects. Much of this review is speculative and based on analogy with living terrestrial arthropods, many of which have changed little since the Carboniferous. Objections can be made to this kind of comparative zoology, especially on the grounds that modern tropical forest communities are qualitatively different from their Carboniferous precursors (e.g., Elton, 1973). But, provided the limitations of such uniformitarian thinking are kept in mind, it can provide models (e.g., of *Arthropleura* as a hollow-lycopod inhabitant and decomposer) that might not otherwise suggest themselves.

Trace fossils, being autochthonous, could yield important evidence of the occurrence and behaviour of Carboniferous terrestrial arthropods, but almost none besides that of *Arthropleura* (Briggs et al., 1979) has been analysed in sufficient detail. More experimental neoichnology is required, especially on the various groups of arachnids, on which little has been published (Alf, 1968; Brady, 1947). Until this has been done, and the limits of variation explored, it will be difficult to interpret ichnocoenoses effectively (Brady, 1947; Rolfe, 1980).

MYRIAPODS AND ARTHROPLEURIDS

Millipedes have long been known in situ from the classic tree-stump fauna of Joggins, Nova Scotia, and they have since been found in a hollow *Sigillaria* tree (Westphalian C) at Florence, Nova Scotia, confirming the ancient detritus-feeding habit of the group. Numerous other records have also been added to the list (Baird, 1958; Förster, 1973; Hoffman, 1963). Many authors have accepted the view that the Carboniferous archipolypod myriapods differed significantly from other millipedes, and that they were amphibious (e.g., Hoffman, 1969).

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Both views have been challenged by Burke (1979), who united the group with the Diplopoda, and this view is followed here.

Centipedes had also long been thought to be present in the Carboniferous, but this view was recently rejected (Hoffman, 1969). Recent work by Mundel (1979) reveals that centipedes, in fact, are present in the Mazon Creek fauna, and known from 15 specimens. Only one of Scudder's species survives, however, *Latzelia primordialis*, which proves to be a scutigeromorph, a group of fast-running surface hunters. A cryptopid is also present, *Mazoscolopendra richardsoni*. Mundel also draws attention to an overlooked record of a geophilomorph? from eastern Canada. This restores a significant invertebrate carnivore to the Palaeozoic fossil record. Much work remains to be done on Carboniferous and other Palaeozoic myriapods before it will be possible to make much progress in understanding their structure and possible habits.

MILLIPEDES

Many adaptations of modern millipedes (Manton, 1977, p. 352–368) had been developed by the Carboniferous, according to Kraus (1974) and Burke (1973, 1979). Thus, the julomorph head-off burrowers are represented by *Xyloius*, *Nyranius*, and *Isojulus*; the shallow-burrowing pill-millipedes, with their ability to enrol tightly, by *Amynilyspes* (Richardson and Johnson, 1971, fig. 3b), *Archiscudderia*, and *Glomeropsis*; wedge-burrowers by *Myriacatherpestes inequalis*; and flat-backed litter-splitters by forms such as *Arthropleura*, *Palaeosoma*, and possibly the laterally-spined form *M. clarkorum* (Burke, 1973, p. 22, fig. 7). In other spined forms, the subdorsal spines are greatly elongated to form defensive spikes, as in *Euphorbia*, *M. ferox*, and *Acantherpestes major*. The latter is known from fragments up to 235 mm long (Kraus, 1974, p. 16), although it must have been at least 300 mm long in life (Scudder, 1882, p. 151). Kraus points out that these forms were unable to burrow in rotten wood or humus. With their large compound eyes, they probably lived at the surface and climbed on plants, whence they fell into water to be preserved; none is now thought to have been originally amphibious. Such prickly creatures would be difficult for predators to cope with. Some of the spines on one specimen of *Acantherpestes major* (pl. 1A–C) from the Upper Pennsylvanian of Kansas (Zidek, 1976) are hollow and broken off, and others seem to show crushing, proving the effectiveness of such spikes.

Apertures of repugnatorial glands (ozopores) have not been seen on the heavily spined forms. They may be located on the ventral side of the paratergal spines as they are, unusually, in the Recent spined polydesmoids (Loomis and Hoffman, 1962). We know as little of the habits of these rare living forms as we do of the fossil genera. Ozopores have been recorded on other Carboniferous millipedes, but this interpretation has been challenged (Hoffman, 1979, p. R582) and restudy is required. In

Recent millipedes, the repugnatorial glands produce irritant exudates, which "in some of the larger tropical forms can be discharged in the form of a fine jet or spray. The maximum recorded achievement was a double salvo from the juliform *Rhinocricus lethifer* in Haiti, which sent its discharge 71 cm on one side and 84 cm on the other, the droplets falling fanwise around the body" (Cloudsley-Thompson, 1978, p. 36). Such repugnatorial fluids have a strong caustic action and can deter, or even blind, predators. Lizards will turn away at an inch or so from *Tachypodoiulus*, and one which persisted eventually rejected the prey and rubbed its mouth in sand (Cloudsley-Thompson, 1949, p. 139). Amphibians and birds are their most effective predators today. They are a constant diet item of the American toad; 77 were found in one toad's stomach, and 10%, by bulk, of the food of this species is composed of millipedes. Nevertheless, enemies do not play a large part in the ecology of myriapods; their numbers are chiefly governed by the physical conditions of the environment (Cloudsley-Thompson, 1949). Millipede fragments have been noted in coprolites from Joggins and Mazon Creek (Fisher, 1979, p. 380).

ARTHROPLEURIDS

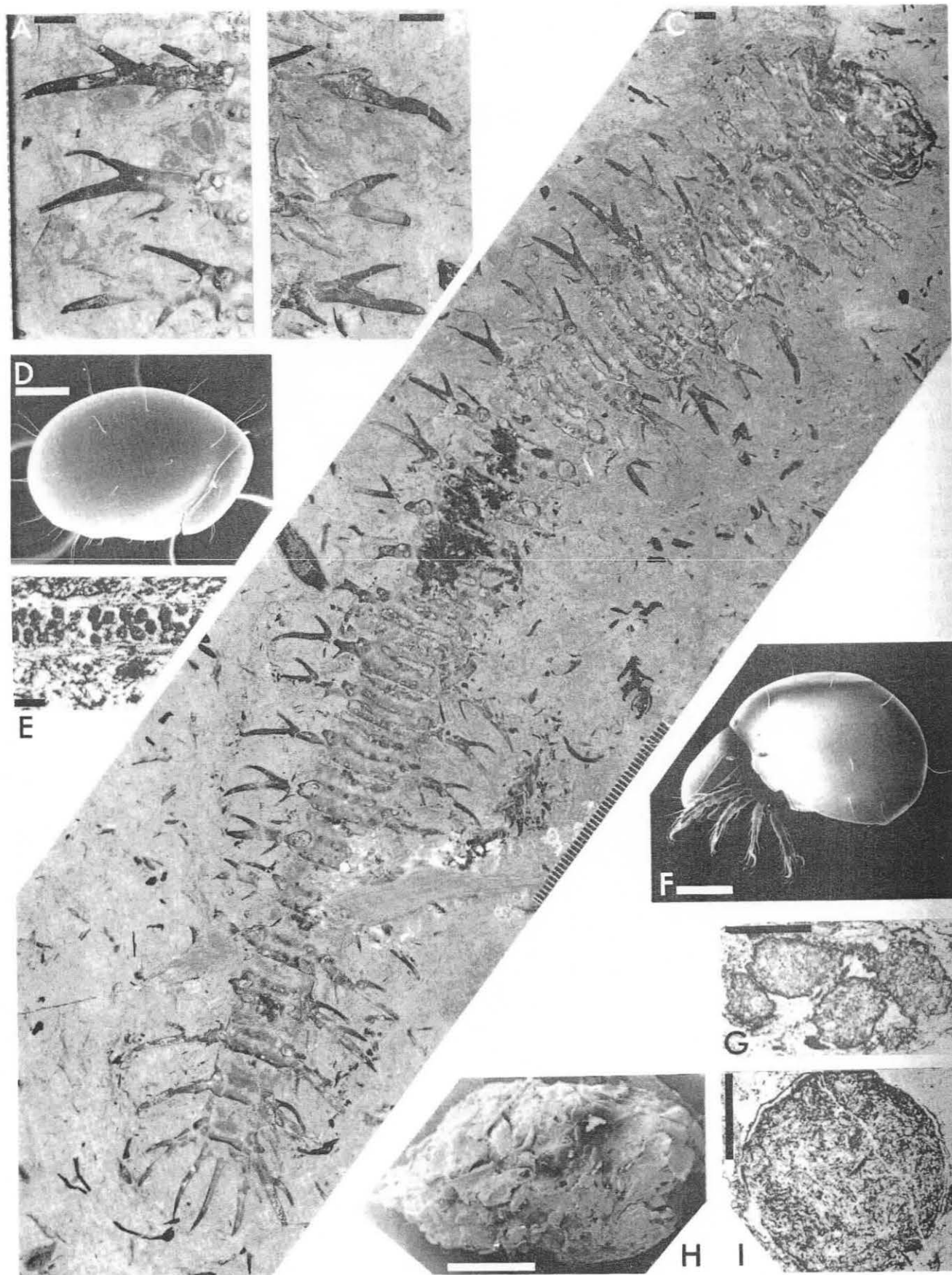
Opinion differs as to whether the 1.8-m-long *Arthropleura* represents a group within the Myriapoda (Demoulin, 1969; Rolfe, 1969), or whether it constitutes a distinct uniramian group and thus "is no close relation of any existing myriapod group" (Manton, 1977, p. 27). Like the flat-backed millipedes (Blower, 1955), *Arthropleura* is not mechanically adapted to life within the soil, and it is

PLATE 1. Carboniferous and Recent decomposers, and their faecal pellets

- A–C. Spinose archipolypod millipede *Acantherpestes major* (Meek and Worthen), Upper Pennsylvanian, Hamilton Quarry, Kansas (Hunterian Museum A. 2710). Possible damage by predators: A—tips broken off paratergal spines, x 4; B—crushed spine, x 4; C—complete specimen, x 2, from which details A and C were taken. Scale 20 mm long, calibrated in 0.5 mm.
- D, F. Typical Recent wood-boring box mites, x 100. D—*Phthiracarus anonymus* Grandjean, limbs retracted; F—*P. murphyi* Harding. SEM photographs kindly provided by Dr. B.W. Parry, British Museum (Natural History).
- E. Mite? faecal pellets, filling mesophyll of *Cordaites* leaf from Middle Pennsylvanian coal ball, USA, x 58.
- G, I. Fossil millipede? coprolites, from Middle Pennsylvanian coal balls, USA. G—group of four coprolites, x 4; I—Baxendale type B coprolite in cross section, x 8.
- H. Faecal pellet composed of plant debris, from 250-mm-long Recent juliform millipede *Scaphiostreptus seychellarum*, x 8.

Bar scale 2 mm long except in D–F where it represents 0.1 mm.

Figs. E, G and I, from Baxendale (1979), by permission of the author and The Palaeontological Association.



clearly much too large for such a habit. As in modern tropical forests, the Coal Measures leaf-litter layer was probably only thin and ephemeral (Elton, 1973, p. 95) and could not have provided a suitable habitat for *Arthropleura*. The forest floor would probably have been "largely composed of woody elements at various stages of decay" (Lawrence, 1953, p. 23). This is borne out by the presence of lycopod tracheids within the gut of *Arthropleura* (Rolfe and Ingham, 1967), which indicates that the central woody stele of trunks and branches was being eaten, rather than leaves (Scott, pers. com.). Some living millipedes are not only specialised to burrow into wood but they also feed on it (Miller, 1974, p. 569). The speed with which the pith of *Lepidodendron* was broken down is attested to by the existence of many sandstone internal moulds of trunks. *Arthropleura* may well have sought out and spent much of its time within such hollow rotted trunks, not only for protection from tetrapod predators but also for access to its food of rotting stele fragments. The high humidity of such microenvironments would form a favourable ecological island or refuge (Hurley, 1968, p. 331–332), and also serve as a good natural moulting chamber for *Arthropleura*. In the dry season, some modern millipedes burrow into logs on which they are feeding, seal the entrance with masticated wood, and remain there for two weeks. Because these logs never dry out completely, the animals are protected at their period of greatest stress, when they moult (O'Neill, 1969, p. 582–583). At other times, *Arthropleura*'s flat-backed habit enabled it to split its way through the litter of fallen twigs, branches, and logs on the Coal Measures forest floor (Rolfe, 1969, p. R615). Such a habitat, offering protection from flood, drought, and many tetrapod predators, is shown in the center foreground of Augusta and Burian's reconstruction of a Coal Measures forest (1960, pl. 7). Probably, some amphibians were adapted to seek out *Arthropleura* in this niche, and A.R. Milner (pers. com.) has suggested that *Eogyrinus* is suitably elongated for this purpose. *Pholiderpeton* has also been found inside a hollow lycopod log. *Calligenethlon* from the Joggins tree stumps would also be a plausible candidate.

Manton (1977, p. 234) pointed out that the limbs of *Arthropleura* differ from those of modern myriapods, and may have been only relatively weak. She suggested that *Arthropleura* "scraped on or in a rough, possibly softish substratum," more or less raking its way through such debris. This view is based partly on a misinterpretation of the limb structure, which does seem to have been provided with both pivot and hinge joints (Briggs et al., 1979, p. 286). The discovery of large fossil trackways attributable to *Arthropleura*, from the Namurian of Scotland and the Westphalian of Joggins (Briggs et al., 1979), indicates that *Arthropleura* could "stand cleanly on the ground" (cf. Manton, 1977, p. 234) and could support its body weight outside the litter zone. It seems to have walked across sand-plugged distributary channels on

delta-surfaces (fig. 1), perhaps to take up water during times of water stress. Therefore, it was able to leave its forest habitat from time to time, as do the larger millipedes of present-day tropical forests (Lawrence, 1953, p. 336). In such an open environment, *Arthropleura* would doubtless have been more vulnerable to a wider range of predators than in the forest. The leathery cuticle and sheer size of a fully grown *Arthropleura* would protect it from much predation, although younger instars, and other myriapods, would doubtless succumb. Some Coal Measures tetrapods probably behaved like the modern coati, which "spends the greater part of its effort searching among ground litter and debris for invertebrates, as well as digging them out of the soil, using its sense of smell to locate them. Coatis also tear apart rotting logs to get at sheltering invertebrates . . . they will systematically dissect such logs for frogs, snails, centipedes and the like (mostly sheltering nocturnal species)" (Elton, 1973, p. 94).

The absence of obvious spiracles in *Arthropleura* (Rolfe, 1969, p. R615, R617) and its large size are probably adaptations to reduce desiccation. If a tracheal system existed at all, the spiracles would probably have opened into a vestibule, creating a microclimate insulated from that outside, thereby reducing water loss. Certainly the spiracles did not open on the rosette plates, which Demoulin (1969, p. 2) erroneously interpreted as a device for closing and protecting the spiracles, inasmuch as the whole unperforated surface of the plate is known from many specimens. A similar adaptation exists in desert beetles, in which the spiracles open into a subelytral space. Such a cavity might have existed beneath the K- and B-plates (Rolfe, 1969, fig. 390), as implied by Manton (1977, p. 235). One would expect the aperture of such a cavity to be closable, to control water loss (Edney, 1977, p. 80), and the K-plate is well constructed for such a purpose. Thus, one returns to the older view of the K-plates (Kiemenblätter) as part of the respiratory apparatus, although not as gill plates but as pseudotracheal covers. It is now known (Rolfe and Ingham, in Størmer, 1976, p. 109) that the K-"plate" comprises reflexed cuticle, its inner (dorsal) surface differing in ornament from the smooth, protective outer (ventral) surface, analogous to the eurypterid Blattfuss (Waterston, 1975, fig. 3). Lung-covers may be present over tracheae in arachnids, and tracheae generally are assumed to have evolved independently in at least three or four groups of arachnids (Levi, 1967, p. 571, 573, 577). As both book-lungs and tracheae are present in some arachnids, it is conceivable that, in addition to pseudotracheae, *Arthropleura* had tracheae opening off the pouch beneath the K-"plate". Detailed dissection is required to investigate these possibilities. Such pseudotracheae evolve as the need arises; they do not imply phylogenetic affinity, any more than do respiratory organs in general (Levi, 1967, p. 582). They occur in isopods, land-crabs, and eurypterids (Størmer, 1976).



FIGURE 1. Artist's impression of ca. 0.9 m-long *Arthropleura* leaving its normal coal forest habitat and making a *Diplichnites* trackway across a sand-plugged distributary channel on a delta top. The reconstruction is based on evidence from a Namurian occurrence in Arran, Scotland, where the presence of roots suggests that the channel was already colonised by *Calamites*? (see Briggs et al., 1979).

DECOMPOSITION ROLE OF ARTHROPODS

Little attention has been paid by palaeontologists to the role of decomposition, except by geomicrobiologists (e.g., Moore, 1964, 1966) and palaeobotanists. Perhaps this results partly from the emphasis on the special conditions required for coal formation, in which the accumulation of plant materials is made possible by minimizing the effectiveness of the normal agents of decomposition (Cohen and Spackman, 1977, p. 73). Yet most of the non-carnivorous arthropods of the coal forests were such decomposers, and they provide evidence of the normal forest life in the regimes outside the wet areas of coal formation. Terrestrial arthropods formed part of the diet of higher trophic level consumers, and they, along with other organisms, form the basis of the Carboniferous food webs illustrated by Milner (1980) and Scott (1980). Terrestrial ecosystems contrast with marine ecosystems in that the greatest proportion of primary production passes through the decomposer chain.

HABITATS

Although a wide diversity of terrestrial habitats (e.g., Wallwork, 1976) must have existed in the Carboniferous, little is known about the arthropods of them except in the coal forest. There are three main forest habitats available to Recent arthropod decomposers (Blower, 1955, p. 139–140): (1) on the forest floor and in the aerial parts of vegetation (epigeal); (2) in the floor (litter and soil layers); and (3) under the bark and in the rotten wood of old tree stumps, fallen logs and branches. The last habitat yields one of the richest series of animal communities (Elton, *in* Wallwork, 1976, p. 250). In a modern central Amazonian rain forest, the overwhelming dominance of wood matter in the phytomass is reflected by a relatively large proportion of wood eaters, which comprise 14% of the zoomass. These are composed of only two animal types: termites and beetle larvae (Klinge et al., 1975, p. 117). Because evidence of these habitats has vanished by virtue of its decomposition, one can only conjecture from modern analogues and allochthonous fossils what such habitats were like during the Carboniferous. This has already been hinted at above, particularly in the discussion of myriapods and *Arthropleura*, but one other line of evidence can be considered.

COPROLITES

Although they have probably long been observed in coal balls by palaeobotanists (e.g., Walton, *in* Scott, 1977; Rothwell, pers. com.), coprolites from coal environments have not been recognised as of myriapod and mite origin until recently (Baxendale, 1979; Kubiena, 1955; Scott, 1977). Thus, the bibliography by Häntzschel et al. (1968) contains no reference to these arthropods, yet they were probably the dominant coprolite producers in coal forests. They may also be abundant in Recent peats; Cohen and Spackman (1977, p. 72, 108) found them commonly in all

autochthonous peats of the Everglades mangrove complex. Over half their thin sections of *Rhizophora mangle* peat contained pellets 25–300 μ in diameter, and they were also found in peats of the relatively dry fresh-water tree hammocks. Because such coprolites were only rarely found in peats of the wetter fresh-water environments, mites and millipedes probably were primarily responsible.

The most thorough study of such coprolites is that on Westphalian coal balls by Baxendale (1979), who found that the coprolites ranged in size from 0.5 to 8 mm in diameter. Such coprolites were probably left by millipedes, *Arthropleura* and various insects such as cockroaches (Scott, 1977), because no terrestrial isopods are known from the Carboniferous. It is important to remember that most arachnids, except mites, are carnivorous and hence are liquid feeders. They would produce no faecal pellets containing plant debris (cf. Scott, 1977, p. 64, 66).

MILLIPEDE AND ARTHROPLEURID FAECAL PELLETS

"In places where they are abundant, as in some woodland soils, a humus layer consisting largely of millipede faecal pellets may occur" (Jackson and Raw, 1966, p. 26). Such pellets have received much attention for the important part they play in soil formation (e.g., Webb, 1977). Some of the slightly differing morphologies of the faecal pellets of different millipedes have been illustrated by Paulusse and Jeans (1977).

The size of millipede faecal pellets is dictated by that of the vertical anal slit with its valve-like anal plates that open to emit the pellet (cf. Scott, 1977, p. 66). A large living juliform millipede, *Scaphiostreptus seychellarum*, 250 mm long and 20 mm in diameter, produces faecal pellets 7.5 mm long and 4 mm in diameter (pl. 1H). Taking only the axial region of the body of *Arthropleura* to be comparable with *Scaphiostreptus*, and applying the foregoing proportions, a fully grown *Arthropleura* could have produced a coprolite at least 40 mm in diameter and 75 mm long. That this is conservative is shown by the width of the gut infill of *Arthropleura* (Rolfé, 1969, fig. 386), which is not much less than that of the animal's axis. In the largest animals, this axis must have reached almost 200 mm in width. Such dimensions are far in excess of the Westphalian coprolites recorded by Baxendale (1979) and Scott (1977), which have a maximum diameter of 8 mm. Such coprolites probably came either from small *Arthropleura* or from large millipedes such as *Acantherpestes* or *Palaeosoma*.

Baxendale (1979) found that some coprolites (his type A) contained only one plant or tissue type, for example, spores, as Scott (1977) had previously found; these are probably not of millipede but are rather of insect or other arthropod origin. Others contained fragments of pinnules of the pteridosperm *Alethopteris lesquereuxi*, or outer tissues of cordaite ovules. This may imply partitioning of the food supply among various arthropods, as happens at

the present day (Cornaby, 1977), some arthropods showing a preference for one species of litter over another.

Several factors of modern leaf litter are correlated with acceptance by millipedes, including nitrogen, sugars, and moisture content (Sakwa, 1974, p. 330). Palatability of leaves is known to increase with their age, and this may be due both to the decrease in concentration of leaf polyphenols and to the microbial opening up of the food that takes place during early decomposition (Sakwa, 1974, p. 331). Wood is largely indigestible until it has been partially decomposed, unless the arthropod possesses a suitable gut symbiont. The amount of litter consumed by millipedes is correlated positively with decomposition, the most important source of nutriment for litter eaters being the saprophytic bacteria and fungi that develop on the litter, which acts largely as a substrate. Such microflora increase the lipid, carbohydrate, and protein content and combine cell contents into protein complexes, rendering them accessible to litter eaters by incorporating them into their own substance (Sakwa, 1974, p. 331). This breakdown may occur very rapidly under tropical conditions: "as the wet season progresses, the surface litter is broken down rapidly and so completely that only the very surface of the mineral soil is lightly stained with humus" (Wallwork, 1976, p. 208; see also Moore, 1964, p. 256). Living organisms such as millipedes seem to prefer the brown rot of wood, in which cellulose is removed by putrefaction and bacteria predominate over fungi, to white rot (Wallwork, 1976, p. 245). In the latter case, lignin is removed by the fungi which predominate, and it is known that fungal hyphae can also infect arthropods.

Both Carboniferous (Baxendale, 1979) and Recent (Nicholson et al., 1966) faecal pellets are known to have been invaded by fungi; such fungi may be an important source of calcium for saprophagous arthropods and other soil animals (Cromack et al., 1977). Wieser (1968, p. 499) suggested that such microbial activity in faecal pellets of terrestrial isopods is important in liberating otherwise unavailable heavy metals, which can then be assimilated by coprophagy. Such recycling may have been important in decomposing regions of the coal forests; elsewhere, the accumulator activities of plants, e.g., of lycopods in removing alumina, would result in significant permanent depletion (Moore 1964, p. 268). Other arthropods are known to reingest their own faeces after they have developed a microflora, and the forest floor has been characterised as a giant external rumen for arthropods (Crossley, 1977, p. 52).

The most important role that millipedes play, however, is in the disintegration and comminution of large quantities of litter (Edwards, 1974, p. 539). In this task they may follow, and be followed by, a whole sequence of bacterial, fungal, mite, and other decomposers. Webb (1977, p. 64) proposed that "the balance of large to small arthropod activity in soil systems constitutes a regulating mechanism controlling rates of total decomposition of litter."

MITE MICROCOPROLITES

Much smaller coprolites are known than those mentioned above; they usually have diameters between 30μ and 40μ and often occur in loose aggregates (pl. 1E; Baxendale, 1979; Kubiena, 1955, fig. 14). These were probably defecated by mites resembling the living box mites (Oribatiidae), shown in plate 1D. Mites are known since the Devonian (Rolfe, 1980), and the Recent genus *Hydrozetes* is known from the Jurassic (Sivhed and Wallwork, 1978), indicating the conservativeness of this group, and doubtless of its habits as well. Today, such mites bore into wood and tunnel into conifer needles. Similar occurrences within the mesophyll cavity of the Westphalian *Cordaites* leaf shown in plate 1E, and in a burrow in a *Lepidophloios* leaf cushion (Baxendale, 1979), demonstrate the antiquity of this habit. Such mites are effectively cut off from micro-predators by the packed faecal material (Wallwork, 1976, p. 260). Mites may preferentially attack certain regions of plants before others, and Wallwork (1976, p. 256) records the lenticels of birch bark being burrowed and filled with corky faecal pellets by nymphs of one mite.

DECOMPOSITION

The importance of millipedes as soil producers is obvious. "The end result of all this plant and animal activity is the reduction of the woody tissue to small, partly decomposed particles which become intimately mixed with the surrounding soil after their passage through the gut of earthworms and molluscs. Many of the mites and Collembola, which feed on the wood, subsequently distribute it as faecal pellets deeper in the surrounding soil, where it may be degraded further by micro-organisms" (Wallwork, 1976, p. 249).

EURYPTERIDS

Recent work on the respiratory structures of eurypterids by Størmer, (1976), Waterston (1975), and Wills (1965) culminated in the view that the "eurypterid gill tract might have acted both as gill and pseudotrachea" (Størmer, 1976, p. 143). This discovery was made on one of the most aquatically adapted eurypterids, *Baltoeurypterus*, although similar structures have also been found in the larger more amphibious-looking *Tarsopteryella*. This implies that "several eurypterids at least might have been able to leave the water and stay on land for shorter or longer periods. They may have been able to remain above the supra-littoral zone, and thus be more terrestrial in their habits than the Recent *Limulus*" (Størmer, 1976, p. 143). Such amphibious eurypterids probably lived on sandy and muddy beaches in the early plant thickets on the land beyond. Like modern *Limulus* they probably burrowed, only shallowly, for worms and molluscan prey (Manton, 1964, p. 35), and, like Recent land hermit crabs, they might have fed on seaweed and other plant debris, such carrion as was available, and sick members of their

own species (Kaestner, 1970, p. 329–330). *Euproops danae* has also been suggested to have been amphibious (Fisher, 1979).

GILL-TRACTS

The polygonal meshwork surrounding the minute gill-tract spinules in *Baltoeurypterus* (Wills, 1965, p. 119, pl. 3; Størmer, 1976, p. 139–42, figs. 68–70) is remarkably similar in size and form to the intricately sculptured meshwork covering insect egg-shells (Edney, 1977, fig. 102), and to the star-based spigots of spider book-lung surfaces (Moore, 1976, figs. 11, 13). Størmer, (1976, p. 142) noted similar structures in insects and the pseudotracheae of isopods, and suggested that their function is to retain air and thus prevent water from clogging the finer respiratory canals of insects, isopods, and eurypterids. The significance of these structures may be much greater, however, because in the egg-shells mentioned they function as a plastron (a gaseous gill) permitting the uptake of oxygen even when the egg is covered with water (Edney, 1977, p. 215). Although the spider book-lung spigots doubtless serve to prevent the lamellae from adhering to each other during respiration (Moore, 1976, p. 178), they may also serve to create a plastron when such spiders are submerged. The same perhaps applies to the terrestrial isopods which run a great risk of drowning during the rainy season (Edney, 1968, p. 322–323). All this implies that eurypterid pseudotrachea could also have functioned as a plastron. In turn, this leads to the unlikely suggestion that such eurypterids were largely air-breathers, as the permanent plastron-respirers are usually small. Plastron respiration is only known today among insects and one mite, where “plastron-bearing spiracular gills enable the animal to meet the contradictory requirements of environments that are alternately dry and flooded” (Hinton, 1971, p. 1185). “From the point of view of moisture content, many terrestrial environments differ little from aquatic: they are saturated most or all of the time. To be submerged in water for several hours or even days is not a rare or isolated event but a normal hazard of the environment” (Hinton, 1977, p. 72). Therefore, plastron respiration is commoner among terrestrial than aquatic insects.

The eurypterid spinules are higher than the corresponding Recent structures; this suggests that the plastron may have been thicker, perhaps too thick to function. It must be mentioned, however, that some insect egg-shell meshworks may also be hydrophilic (Edney, 1977, p. 215–216), presumably to combat desiccation; perhaps this is a more likely alternative in the eurypterid gill-tract.

MESOSOMAL ENLARGEMENT

In the light of this new, amphibious view of eurypterids, the enlargement of the first two mesosomites in *Woodwardopterus*, and of at least the first (genital) mesosomite in *Mycterops*, may be significant. It is unknown whether such enlargement takes place by inflation of individual

somites or by ankylosis of several anterior somites (Waterston, 1957, p. 285–286). Some of the *Tarsopterella*-type gill-tract structures (Waterston, 1975) can be discerned in these somites of the holotype *Woodwardopterus scabrosus*; they require study. Terrestrial arachnids have book gills only on the first two opisthosomal segments, even from the time of the early Devonian Rhynie palaeocharinids. “The fossil record indicates that the terrestrial arachnids . . . evolved from aquatic forms breathing with ribbon-like gills or book-gills, [which] were replaced by book-lungs and . . . tracheae” (Størmer, 1976, p. 152). It may be that a parallel development, enlargement of the first two opisthosomites, occurred in some eurypterids as an adaptation to accommodate larger book-lungs or pseudotracheae to enable better respiration on land. Such a criterion, if substantiated, could prove valuable for recognising more fully terrestrial forms. The evolutionary lack of success of the eurypterids in making it ashore, except through their scorpionid relatives, may be correlated with this failure to develop adequate respiratory structures. Among modern arachnids, only the solpugids are fully active, because of a good tracheal system. Other arachnids have a largely incomplete respiratory system (Størmer, 1976, p. 152), which may account for the sluggish behaviour of more ancient members of the group.

SIZE AND LIMBS

There seems to have been a trend for various Old Red Sandstone eurypterids to increase in size (e.g., *Tarsopterella*, *Ctenopterus*, *Pterygotus anglicus*). Such a size increase would reduce desiccation loss by increasing the surface-to-volume ratio, and it would have been selectively advantageous to those eurypterids that were to survive the periodic droughts of the Old Red environment. Large size as a water conservation mechanism occurs in several groups of Recent animals “such as terrestrial members of mainly aquatic groups. It is not coincidental that, even though large size is generally considered a disadvantage in locomotion on land, the largest of free-living flatworms are terrestrial turbellarians, the largest annelids are earthworms and the largest leeches are among those that, in attacking mammals, may be carried on land” (Levi, 1967, p. 579). This relationship may also account for the trend toward large size seen in several terrestrial fossil arthropod groups: scorpions, eurypterids, millipedes, arthropleurids, and insects. Some of these may represent independent attempts at terrestrialisation.

As with crossopterygians (Romer, 1966, p. 86; Størmer, 1976, p. 143), individuals that survived may have evolved adaptations such as the stylonuroid walking limbs in order to migrate to the nearest available waterhole, rather than for any terrestrial ambition. Long stylonuroid legs would also enable their owner to ‘stilt’ like modern scorpions and thereby maintain constant body temperature whilst the ambient temperature rises rapidly (Alexander

and Ewer, 1958). Above a certain temperature range, stiltling no longer protects the animal, and it seeks cover.

With the advent of the less rigorous conditions of the Carboniferous, the need for such a size adaptation would have waned, but the larger stocks may have been pre-adapted for life on land.

JOGGINS AND ITS EURYPTERIDS

This celebrated Westphalian B locality is important in preserving a terrestrial fauna in situ within *Calamites* and *Sigillaria* stumps. It has been authoritatively reviewed by Carroll et al. (1972, p. 64–80) and the arthropods have been discussed by Briggs et al. (1979, p. 286–287). The hollow stumps were buried, creating pit-falls that are thought to have sampled the truly terrestrial fauna. "With the exception of one or two coelacanth scales (which may have been someone's dinner) no fish are known from the stumps, nor are there any strictly aquatic amphibians" (Carroll et al., 1972, p. 67). Besides the land snail *Dendropupa*, the remaining invertebrates are all arthropods. Eight millipede species have been recorded as abundant in the trunks and millipedes may well have sought out tree stumps both as a damp refuge and as a food substrate. In turn, they were preyed upon to some extent (their abundance suggests not greatly—Carroll, pers. com.) by the tetrapods, as millipede somites and other cuticles are recorded from tetrapod coprolites (Dawson, in Scudder, 1895). Two arachnids, the anthracomartid *Coryphomartus triangularis* (Petrunkevitch) and the whip-spider *Graeophonus carbonarius* Scudder (Petrunkevitch, 1913, p. 69, 101; 1953, p. 60, 99), doubtless came from tree-trunks (Carroll, pers. com.).

Many fragments of eurypterid cuticle that have been compared with *Dunsopteris*, *Hibbertopteris*, and *Vernonopteris* (Waterston, pers. com.; Briggs et al., 1979, p. 287) occur within the tree stumps. Dr. J. Dalingwater confirmed the eurypterid nature of the cuticle by SEM study and compared the cuticle microstructure with that of *Mycterops*? (Dalingwater, 1975). These eurypterid genera are morphologically unusual forms, all of which, except *Hibbertopteris*, are known only from fragments of thick cuticle (Waterston, 1957; 1968) from non-marine deposits. This incompleteness may be due to the habit of eating their own exuviae, to enable the formation of new cuticle, as does the modern terrestrial coconut crab *Birgus* (Harms, 1932, p. 175, 280). Such land crabs grow to largest size where the most abundant fruits are found; but even so, *Birgus* needs to eat fish and crab meat occasionally. It will resort to cannibalism if deprived of meat (Harms, 1932, p. 175, 279). This suggests another possible reason for the fragmentary finds of these presumably more carnivorous eurypterids.

Hibbertopteris, however, has short stubby limbs and is noticeably hexapodous. It would seem to be better adapted for movement on land despite its bulky opisthosoma, and it has sensory anterior appendages (Waterston,

1957). *Birgus* shows a similar adaptation, in contrast to most coenobitids that have four pairs of walking legs, and becomes hexapodous in its most active, adult stage (Harms, 1932, p. 282). The bulkiness of *Birgus* is deceptive, as it can show considerable agility on land (Harms, 1932, p. 170); this may also have been true of similarly bulky-looking eurypterids such as *Hibbertopteris*. It is doubtful, however, that any eurypterid climbed trees like *Birgus*, as J.M. Clarke jokingly suggested after the presentation of O'Connell and Grabau's paper on the riverine habit of eurypterids (Caster, pers. com.).

With the possible co-evolutionary rise of predatory tetrapods, such feeble attempts to terrestrialise would be doomed to failure; this might explain the demise of these large eurypterids in the Carboniferous, similar to the large pterygotids earlier in the Devonian (Waterston, 1968).

How did such eurypterid fragments get into the hollow tree stumps? Were they carried there by predatory tetrapods, as were the coelacanth scales? Or did eurypterids fall into the pits whilst crawling clumsily about the new land surface? They might also have sought out such refuges to prevent desiccation, or in order to moult, as does the living *Birgus* (Harms, 1932, fig. 37). Finally, were they washed in by flooding of this 'bayou' country, giving mixed aquatic and terrestrial biotas, in death if not in life, as K.E. Caster suggests (pers. com.)? In favour of this latter explanation is Woodward's (1918, p. 464) point that the stumps are occasionally found with *Spirorbis* ("more characteristic of swamp facies," Calver, 1968, p. 163) attached both to the inside and the outside of the bark. Lacking a most detailed palaeoecological study of a stump, it is impossible to decide this point. However, the overwhelmingly terrestrial aspect of the rest of the fauna, stressed by Carroll et al. (1972), favours the second explanation.

ARACHNIDS

"Arachnids today comprise the dominant invertebrate carnivores on land" (Manton, 1977, p. 15), and their Carboniferous ancestors were probably identical in this respect. As with the cryptic fauna of present-day forests, "there is no question of the carnivorous orders feeding exclusively on the herbivorous ones. . . . Carnivorous groups rather prey on other carnivorous orders and in a free-for-all encounter, overcome any individual which is of suitable size" (Lawrence, 1953, p. 307). Spiders in particular, probably like arachnids in general, are their own worst enemies (Wanless, pers. com.).

SPIDERS

Inward-striking (di axial) fangs are known from two families of Carboniferous spiders, indicating their ability to kill insect and other prey on leaf surfaces and in flat cavities such as beneath bark (Petrunkevitch, 1952, p.

113). These families resemble Recent arachnomorph spiders, but details of their spinnerets are unknown (Petrunkévitch, 1953, p. 100). Hence, spiders with the ability to trap insects aerially by orb-webs are not definitely known until the Tertiary. The possible absence of such efficient webs may partially account for the instant success of the Carboniferous insects, which reach their maximum diversity in the Permian (Carpenter, 1977), because aerial predators other than insects are not known until the Triassic. Older groups of spiders, the liphistiomorphs and mygalomorphs, possessed downward-striking (paraxial) jaws for striking prey on a firm substrate: on the ground or on tree trunks. Liphistiomorphs include the trap-door spiders of today, and the 'living fossil' *Liphistius*. *Liphistius* burrows have about eight long straight threads that serve as trip-wires, radiating downward from the rim of the burrow, indicating the passage of crawling invertebrates (Bristowe, 1975, p. 115). Pit-fall studies indicate how abundant such prey is (Wanless, pers. com.), and the spider has only to rush out and overpower the victim. Predation by such primitive hunting spiders (and, possibly, early amphibians and insects—Smart, 1967, p. 116) upon early wingless insects may have been one of the main factors leading to the evolution of insect wings. "When their prey took to the air to escape, spiders evolved aerial webs as a means of trapping it in flight" (Cloudsley-Thompson, 1968, p. 186; 1975a, p. 192; 1975b). This escape by flight may well have taken place under the impetus given by the advent of late Devonian trees, which provided not only a launching pad, but also a new, tree-top ecosystem (Kevan et al., 1975; Scott, 1980). It is worth recalling that the high canopy of modern tropical rain forests contains a little-known but large biomass not only of insects, but also of large mygalomorph and web spiders, as well as millipedes (Elton, 1973, p. 91). It seems likely that many arachnid predators pursued their insectan prey up trees as the insects and a high-canopy ecosystem evolved during the Upper Devonian–Carboniferous, even though this may have been simpler and less sophisticated than the present tropical forest ecosystem (Elton, 1973).

OTHER ARACHNID GROUPS

Most of the other living orders of arachnids are also known from the Carboniferous, by which time their fundamental evolution was completed; there has been little since (Petrunkévitch, 1953, p. 115). Of the 16 orders known from the Carboniferous, 11 survive to the present day (Petrunkévitch, 1955; Savory, 1977, p. 97). One such group is the Thelyphonida (or Uropygi) which includes the modern vinegaroon, a form practically unchanged morphologically from the Carboniferous *Prothelyphonus*, known from both Mazon Creek and Czechoslovakia. Modern thelyphonids eat insects, centipedes, woodlice, worms, and slugs (Cloudsley-Thompson, 1968, p. 146).

Living solpugid arachnids kill and eat insects, spiders, scorpions, and lizards using "the most formidable jaws in

the animal world" (Savory, 1977, p. 236). In turn, they are preyed upon by lizards and other reptiles, as well as by birds and mammals (Cloudsley-Thompson, 1968, p. 116). They are the most active of living arachnids and one of those most independent of atmospheric moisture (Lawrence, 1953, p. 139). One fossil solpugid, *Protosolpuga* from the Westphalian of Mazon Creek, is known.

Plump ricinuleid arachnids live today much as their Carboniferous ancestors must have done, skulking motionless under rotten logs, behind leaf fronds on wet mud, and in wet leaf-axils (lamine leaf-bases are known since the Devonian *Archaeopteris*), emerging only to catch and eat living spider and insect prey (Cooke, 1967; Pollock, 1966, 1967). They illustrate very well how such terrestrial arthropods take advantage of plants to control their own environment. By remaining in the shade of large leaves (the laminate leaf evolved in the Carboniferous) such arachnids manage to keep their temperature down in tropical climates. Plants act as windbreaks, with locally humid niches, so arachnids are able to conserve moisture that otherwise would be lost by transpiration across their cuticles, as they lack the wax layer typical of many terrestrial arthropods.

Many fossil arachnids were blind, including the whole order Anthracomartida. In some cases this correlates with their nocturnal habit, but "the special conditions of humidity, temperature and light of the interior of rain forests are all intensified and reach their maximum on the forest floor: the temperature is practically uniform, the humidity always at or near saturation point and almost total darkness prevails" (Lawrence, 1953, p. 53). In these situations, eyes are of little value, and a variety of sensory devices has been evolved by various terrestrial arthropods. Thus, scorpions have sensory hairs (trichobothria) on their pedipalps, which detect minute air currents caused by the movement of prey. The pedipalps are extended like antennae and the scorpion advances, supported by the hind legs with claws open and extended, tail raised: the act of prey capture is almost defensive (Cloudsley-Thompson, 1968, p. 92).

The scorpions are unusual among arachnids in having become largely extinct. According to one classification, only one superfamily survives today of the nine Palaeozoic superfamilies (Savory, 1977, p. 97). Characters used to classify scorpions reflect the nature of the respiratory organs and the preoral chamber, and thus probably reflect the degree of terrestriality. Therefore, extinctions may indicate a sequence of unsuccessful attempts to terrestriality. Most Carboniferous and earlier scorpions are now thought to have been aquatic or amphibious (Størmer, 1963, 1970, 1976; Waterston, 1975, p. 252); the first truly terrestrial scorpion with stigmata is *Palaeopisthacanthus*, from the Westphalian of Mazon Creek. *Gigantoscorpion*, a scorpion 500 mm long from the Lower Carboniferous of Scotland (Størmer, 1963; 1976, p. 153), is suggested to have been amphibious because of its

plantigrade feet, the presence of setae rather than trichobothria, and the nature of the ventral plates concealing the gills. Further details of the mode of life of Carboniferous scorpions may be found in the major review by Kjellesvig-Waering (1985).

Carboniferous scorpions probably fell prey to early tetrapods, much as Recent ones do to lizards and snakes (Cloudsley-Thompson, 1968), although they may have formed only a supplementary item of the diet (Romer, 1958, p. 367). They have been recorded from Mazon Creek coprolites (Fisher, 1979, p. 380).

The enigmatic, large *Cyrtoctenus* must be mentioned, as it bears pectine-like organs resembling those of scorpions. Because of its unique characters, Størmer and Waterston (1968) referred it to a new order of eurypterids and thought it must have been aquatic because of its large size. This serves as a reminder that there must have been many other amphibious and terrestrial arthropods, of which even less is known.

POPULATION STRUCTURE

Since the time of Bateson, modern tropical forests have been known to be prolific in numbers of species, yet they show low population densities of most species. Elton (1973, p. 95–97) attributes this to the great preponderance of predators in the rain forest. For example, one fauna contains 34% spiders and 12% Opiliones, with army ants playing a very important role. Low density, Elton suggests, is one significant adaptive response in the face of such predation; alternatives are the adoption of nocturnal habits, extinction, or the attainment of perfection in defence. The latter is a continuously evolving process, analogous to the missile/anti-missile race, and Elton (1973, p. 99) therefore has suggested that in many respects living invertebrates of this environment may be evolutionarily at the 'end of the road'. Consequently, the present tropical ecosystem might not be a suitable uniformitarian model for the study of living fossil analogues of Carboniferous arachnids, as it can be seen as the fragile end product of evolutionary interaction between predator and prey since the Carboniferous. However, there is some slight evidence to suggest that the high species diversity, possibly coupled with low density, may have been attained by the Coal Measures terrestrial arachnids.

The most prolific Westphalian arachnid faunas are those of Mazon Creek (Westphalian D) and the English Midlands localities of Sparth Bottoms (Westphalian A), Coseley, and Shipley (both Westphalian B). Of the 79 arachnid (including amphibious scorpion) species described (43 from Mazon Creek), 50 are known only from single specimens. An additional 8 species are known both as singletons from one locality, and also from one or more specimens at another locality. None is known from more than two localities. The number of specimens recorded as being in collections, and which comprise the 28 species

known from more than 1 specimen, ranges from 2 to 18 specimens, but with a mean of 3.5 specimens (based on 24 occurrences). This analysis is based on the record published up to 1953 (Petrunkévitch, 1913, 1949, 1953). It is likely that the picture has since changed as a result of the new collections assembled by the Field Museum of Natural History. If the above generalisation holds any truth, such collections might be expected to contain a high proportion of new arachnid species.

Such arachnids are the rarest of all in the Mazon Creek Braidwood fauna, forming only 0.2% of specimens (Richardson and Johnson, 1971, p. 1232). It is difficult to evaluate how much of the low density of the Braidwood arachnids is due to the inevitable rarity of such fully terrestrial fossils, after their transport into the marine delta complex, and how much is a reflection of initial low density in the forest fauna. But the diversity seen within the presumably random sample preserved in the delta sediments implies an even greater diversity in the original forest population sampled. The presence of 18 specimens of *Architarbus rotundatus* (Petrunkévitch, 1949, p. 166) suggests that it is not impossible for large numbers of one species to be preserved. Had the diversity been lower, more specimens of fewer taxa would be expected, although statistical comparison of the existing samples with the populations from which they must have been drawn is required for more objective assessment.

Since the above was written, however, E.S. Richardson has pointed out to me that many of Petrunkévitch's taxa can be shown to be synonymous, and that this is also shown by Kjellesvig-Waering's unpublished review of the phalangiotarbid. This would clearly invalidate the figures given above, and further detailed analysis is required.

PALAEOBIOGEOGRAPHY

Milner and Panchen (1973) and Panchen (1977) have shown that terrestrial tetrapods of the Westphalian coal swamps are common to both Europe and America, providing additional evidence for the formerly united land-mass of Laurasia. A faunal divergence can be detected in the aquatic forms, which becomes exacerbated by the Stephanian-Permian, which those authors attribute to the Appalachian/Caledonian and Hercynian mountain barriers, and to the drying out of the coal swamps. Such a difference might also be expected in the arthropod faunas. *Arthropleura*, for example, has long been known to transcend this barrier (Rolfe, 1969), and at least some of the millipedes do so also (Burke, 1973; 1979).

Mazon Creek yields the largest, most diverse fauna as a basis for comparison of Westphalian D arthropod faunas. No less than 81% of the 170 invertebrate genera are terrestrial arthropods (58% insects, 18% arachnids, 5% myriapods), according to Horowitz and Richardson's 1978 computer printout of this fauna. A rapid, superficial comparison of the arachnids of this fauna with those of the Westphalian D Nýřany locality of Czechoslovakia

(Rolfe, 1980) served only to show that the latter fauna is insufficiently rich in terrestrial arthropods to permit detailed comparison. If the older Westphalian localities of the English Midlands (Sparth Bottoms, Westphalian A; Coseley and Shipley, Westphalian B) are added to the Nýřany records, a richer fauna results and comparability with Mazon Creek improves, although results are not comparable with the more refined analysis of the tetrapods.

Analysis of the published record indicates that nine arachnid families (and eight genera) are common to the European and American faunas; six families are confined to Europe and eight to North America. One of the two arachnids from another locality, the Westphalian B Jogjins site (on the European side of the barrier—Milner and Panchen, 1973, p. 362), exemplifies this link. The species, *Graeophonus carbonarius* Scudder, is known from Mazon Creek (Petrunkévitch, 1949, p. 270), and the genus also occurs at Coseley. The only other arachnid from Jogjins, *Coryphomartus triangularis* (Petrunkévitch), is an anthracomartid—a family known both from Europe and America. That the similarity is not more striking may be due to the fact that not all European and American faunas have been considered, that four Westphalian faunas, covering about 10 million years time (Milner and Panchen, 1973, p. 360), have been lumped together, and that no refined attempt has been made to select localities which are ecologically comparable.

Comparison of Carboniferous aquatic arthropods, the malacostracan crustaceans of Europe and America (Brooks, 1962, 1969; Rolfe, 1969; Schram, 1974a, 1974b, 1978, 1979), yields an even higher degree of similarity. Twelve families occur in common, with only three others being restricted to Europe and five to America. Here again, the lumping together of Carboniferous faunas is too coarse a procedure, and careful refined analysis would be worthwhile. Schram (1976) has already drawn attention to the ecological similarity of several Carboniferous crustacean assemblages. There need be no close analogy of the fresh-water to marine crustacean faunas with the coal-swamp amphibian faunas, however, because the former are derived from a fully marine stock that persisted throughout the Carboniferous and probably was able to be spread far and wide by planktonic larvae. There are insufficient Stephanian-Permian arthropod localities to enable the Milner and Panchen model of increased aquatic divergence to be tested at the critical period.

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